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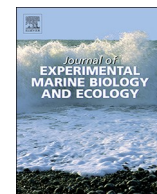
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The interactive role of predation, competition and habitat conditions in structuring an intertidal bivalve population

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ABSTRACT

Habitat characteristics, predation and competition are known to interactively drive population dynamics. Highly complex habitats, for example, may reduce predation and competition, allowing more individuals living together in a certain area. However, the strength and direction of such interactions can differ strongly and are context dependent. Furthermore, as habitat characteristics are rapidly changing due to anthropogenic impacts, it becomes increasingly important to understand such interactions. Here, we studied the interactive effects of predation and competition on common cockle (*Cerastoderma edule*) recruitment, growth and survival under different habitat characteristics in the Wadden Sea, one of the world's largest intertidal ecosystems. In a predator-exclosure experiment, we manipulated cockle densities (100 vs. 1000 individuals m⁻²) and shorebird predation at two sites differing in habitat characteristics, namely at the wake of a blue mussel bed (*Mytilus edulis*) and at an adjacent sandy site. We found that recruitment was higher in the mussel-modified habitat, most likely due to reduction of hydrodynamic stress. Although bird predation strongly reduced recruit density, the combined effects still yielded more recruitment at the vicinity of the mussel bed compared to the sandy area. Furthermore, we found that high cockle densities combined with high densities of other potential prey (i.e. mussels) at the mussel-modified site, mitigated predation effects for adult cockles. Apart from these positive effects on adults, mussel-modified habitat reduced cockle growth, most likely by reducing hydrodynamics in the wake of the mussel bed and by increasing inter-specific competition for food. Our study experimentally underpins the importance of habitat characteristics, competition and predation in interactively structuring intertidal communities.

1. Introduction

A substantial part of ecological theory concerns the role of interactions between organisms in determining population and community dynamics. Out of these interactions, predation, competition and their interactive effects received most attention, as they are believed to be crucial in structuring natural communities (e.g. Paine, 1966; Schoener, 1983; Chase et al., 2002). However, the strength of these interactions and their effects on the community will often depend on general habitat

characteristics. For instance, habitat complexity and quality have been demonstrated to potentially affect the impact of predation (Almany, 2004; Warfe and Leon, 2004). Additionally, both intra- and interspecific competition intensity often depend on habitat characteristics such space or resource availability. Yet, despite the fact that predation, competition and habitat characteristics are all recognized as important structuring mechanisms for communities, their combined effects on population dynamics have hardly been investigated thus far (see for example Olff et al., 2009).

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Apart from a fundamental scientific perspective, the urgency to investigate these interactive processes is increasing as habitat characteristics in many ecosystems are rapidly changing due to the anthropogenic impact, thereby potentially altering competition, predation and the interaction between them. Of all anthropogenic ecosystem disturbances, deforestation of tropical rainforests and desertification of arid ecosystems probably received most public attention. However, human disturbance is also very much apparent in coastal ecosystems, where stressors like global warming, eutrophication, altering of hydrology, habitat destruction and overfishing seriously degraded habitat quality, resulting in (local) declines or extinctions of numerous marine species (Harley et al., 2006; Lotze et al., 2006).

The Wadden Sea – one of the World's largest intertidal ecosystems – is an ecosystem where anthropogenic disturbance over the last centuries has resulted in habitat degradation and associated species losses (e.g. Lotze et al., 2005; Eriksson et al., 2010; Compton et al., 2016). More recently, mechanical dredging resulted in a decline of habitat quality for bivalves and their associated predators. Mechanical dredging for cockles (*Cerastoderma edule*) and mussels (*Mytilus edulis*), for example, altered sediment conditions and caused direct declines of bivalve stocks. Moreover, the removal of cockles and mussels also disrupted intra- and interspecific facilitation and habitat modification processes, thereby hampering recovery of bivalve stocks and further degrading sediment quality (Piersma et al., 2001; van Gils et al., 2006; Donadi et al., 2013a; van der Heide et al., 2014). Consequently, the combined direct and indirect dredging effects negatively affected the distribution and survival of predators such as a red knots *Calidris canutus* and oystercatchers *Haematopus ostralegus* (Verhulst et al., 2004; van Gils et al., 2006; van der Zee et al., 2012). Apart from such bottom up effects, however, it is likely that the change in predator abundances in turn also cascades down into the system where disruption did not take place, as predation by species such as red knot have been demonstrated to significantly impact prey populations (van Gils et al., 2009; van Gils et al., 2012).

Here, we studied the interactive effects of predation and intraspecific competition on an intertidal cockle population at adjacent sites with contrasting habitat characteristics, that are both typical for Wadden Sea condition in the intertidal. One of the sites was located on a sandy intertidal flat, characterized by sediments with large grain sizes and low natural cockle densities. The other site was located in the wake of a mussel bed, where previous work showed that the bed alters sediment conditions through attenuation of hydrodynamics and pseudo-faeces deposition, resulting in silty sediment with a high organic matter content (van der Zee et al., 2012; Donadi et al., 2013a; Donadi et al., 2013b; van der Zee et al., 2015; Eriksson et al., 2017). These environmental modifications in turn enhance the settlement of large numbers of cockles, making this site an important feeding ground for many avian predators (van der Zee et al., 2012; Donadi et al., 2013a; Donadi et al., 2013b). Because recruitment is facilitated, cockles may experience enhanced competition for food with conspecifics due to increased densities. Additionally, the elevated cockle densities can lead to increased aggregation of molluscivore shorebirds, such as oystercatchers (*Haematopus ostralegus*) (van der Zee et al., 2012) and red knots (*Calidris canutus*) (van Gils et al., 2005). Although higher bird densities can enhance predation pressure, the high cockle density and the presence of mussels as an alternative prey may at the same time mitigate the effects of increased bird densities due to the alternative prey options. By manipulating cockles densities and predation at two sites with contrasting environmental conditions, we tested the following hypotheses: (1) by reducing the number of prey, shorebirds alleviate competition among the remaining cockles thereby stimulating cockle growth, (2) predation by shorebirds decreases survival of bivalve recruits and (3) the effect of predation and intraspecific competition are dependent on their environmental setting. To test our hypotheses, we crossed two adult cockle densities with shorebird exclosure treatments, and added tagged cockles to monitor growth at a sandy and muddy site

on the intertidal flats of Schiermonnikoog. After 1 year, we ended the experiment and determined cockle survival, recruitment and growth.

2. Materials and methods

2.1. Study system

The Wadden Sea is a coastal ecosystem, situated in the Southeastern part of the North Sea (Fig. 1). It is characterized by highly dynamic and productive tidal flats and is considered as one of the largest (8,000 km²) and most important intertidal ecosystems in the world (Wolff, 1983; Reise, 2005; Wolff, 2013). Due to its productivity, the Wadden Sea support large numbers of invertebrates, fish and shorebirds (Zijlstra, 1972; Beukema, 1976; Wolff, 1983; van de Kam et al., 2004). Reef forming blue mussels are well-known ecosystem engineers that create hard substrate, reduce hydrodynamics and modify sediment conditions by depositing large amounts of (pseudo-)faeces (Kröncke, 1996; Donadi et al., 2013a). Especially in soft-bottom ecosystems like the Wadden Sea, effects on hydrodynamics and sediment conditions can extend far beyond the bed itself, up to distances of several hundreds of meters (Kröncke, 1996; van der Heide et al., 2012; Donadi et al., 2013b).

2.2. Experimental design

The study was conducted at 0.5 m below mean water level (exposed during low tide for ~30% of time) in the eastern Dutch Wadden Sea, south of the island of Schiermonnikoog. The first out of two study sites was situated 100 m coastward of a mussel bed (site Mussel, 53°28.127' N - 6°13.463' E). This area was characterized by silty organic matter-rich sediment, and reduced hydrodynamic conditions (Donadi et al., 2013a). The other site was located at ~500 m from the first site with the same tidal elevation, but out of the influence range of the mussel bed, and was therefore typified by sandy sediments and served as a control site (site Sand, 53°28.117' N - 6°13.938' E) (Donadi et al., 2013a). Both sites were chosen based on previous studies that successfully demonstrate that this area is highly suitable to investigate the effects of habitat characteristics on multiple interaction types (van der Zee et al., 2012; Donadi et al., 2013a; Donadi et al., 2013b; Donadi et al., 2015; van der Zee et al., 2015). At the start of the experiment in May 2010, the mean background cockle density was 65 nm⁻² at the mussel site and 0 nm⁻² at the sandy control site.

We manipulated predation pressure by establishing 12 1-m² bird

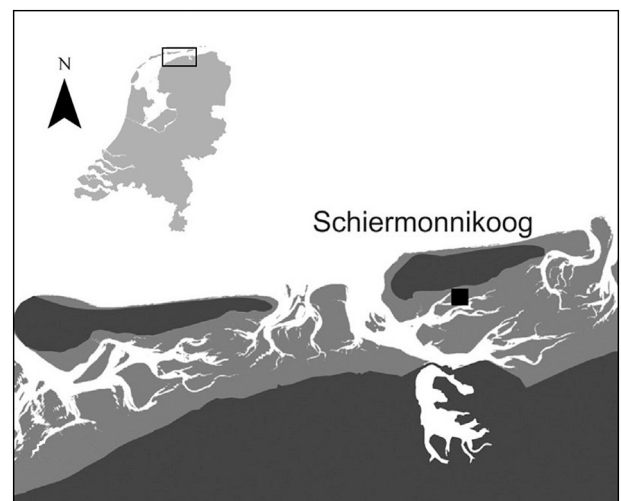


Fig. 1. Map with location of the experimental site in the Dutch Wadden Sea at Schiermonnikoog (black square). White areas represent water, intermediate gray areas represent tidal flats exposed during low tide and land is represented by dark gray.

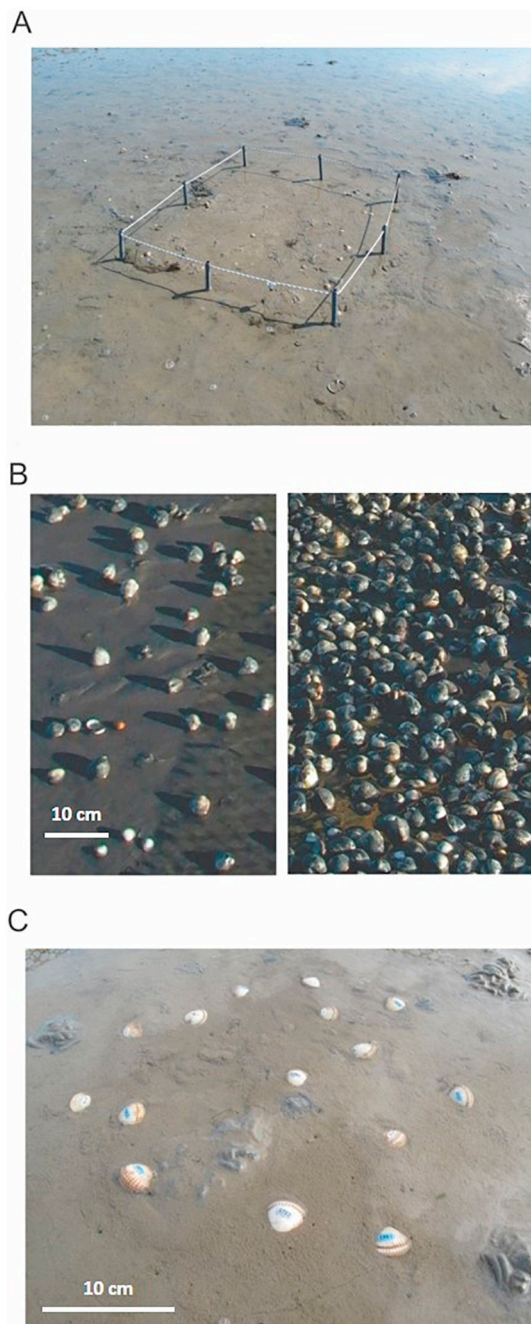


Fig. 2. Overview of a shorebird exclusion (1 × 1 meter) (A), treatment densities: 100 and 1000 cockles m^{-2} (B) and the added tagged cockles (C).

exclusions and 12 control plots at both sites. Exclusion and control plots were paired with a distance of 4 m between pairs and a distance of 10 m between replicates. Each exclusion consisted of 8 PVC-poles (0.5 m long) that were inserted in the sediment to a depth of 0.4 m and aligned in a square of 1 m^2 . A nylon rope connected the tops of the poles thereby acting as a fence (Fig. 2A) to keep birds out but note that crabs can enter the plot (see method: van Gils et al., 2012). Control plots were marked by two small PVC-poles. The plots were checked regularly in the following year and macroalgae and other fouling was removed if present.

Next, we crossed the exclusion treatments with two cockle densities by adding either 75 or 975 adult cockles (Fig. 2B) to each plot in May 2010, yielding a total of 6 replicates of each treatment per site. Cockles for the addition (> 3 yr old; > 25 mm shell length) were collected from

a nearby mudflat by hand-raking. To monitor cockle growth, we also added 25 tagged young cockles to each plot, yielding a total of 100 and 1000 cockles m^{-2} for both density treatments. The 1200 young cockles (~2 yr old; 12 to 26 mm shell length) needed for tagging were collected by hand-raking and immediately transferred to tanks with aerated natural seawater in the laboratory. Here, shell length of each individual was measured to the nearest 0.01 mm with a vernier caliper, and tagged with a polyethylene label (Hallprint glue-on shellfish tags, Australia; Fig. 2C) glued to the shell with cyanoacrylate glue. No mortality was observed due to experimental manipulation. The tagged cockles were added to the experimental plots within 24 h after collection.

One year after the start of the experiment (May 2011), all cockles were recollected by hand-raking and afterwards the sediment of the plot was sieved over a 1 mm mesh. Shell length of recaptured tagged cockles was again measured to nearest 0.01 mm. Untagged individuals were divided into two age-classes – recruits (cockle juveniles that survived their first winter after settlement in 2010) and adults (> 3 yr old) – after which they were counted.

Although experimental setups with similar constructions have proven to work very well in excluding birds without changing abiotic conditions in the Dutch Wadden Sea (van Gils et al., 2003), we nevertheless tested for possible effects on hydrodynamic conditions (cumulative effects of water flow and wave force) by measuring % weight loss of plaster cylinders (Thompson and Glenn, 1994; Donadi et al., 2013a). Besides to possible enclosure effects, the placement of plaster cylinders on all treatments also allowed for the testing of cockle density and site effects. Cylinders (6.3 cm long, 2.4 cm diameter) were made by molding gypsum (Knauf B.V., Utrecht, The Netherlands) around steel nails after which they were dried, weighted, and placed in the field for four consecutive tidal cycles in September 2010. Cylinders were placed in the middle of a plot and randomly in four of the six replicates per treatment ($4 \times 4 = 16$ per experimental site, in total 32). After collection, cylinders were again dried (24 h, 30 °C) and weighed. The loss of dry weight was used as a relative measure of hydrodynamic stress (Donadi et al., 2013a).

Finally, molluscivore shorebird abundance was measured in a 25×100 m plot, surrounding each experimental study site. The two areas were marked with PVC poles and birds were counted from a distance of 150 m, using a telescope (zoom ocular 20–60 ×; ATM 80 HD, Swarovski, Absam, Austria). By counting half an hour after the water retreated from the plots until half an hour before the water inundated the plots again, we excluded shorebirds that foraged on pelagic or epibenthic species (i.e. shrimp, fish) and thereby focused only on endobenthic species as prey item. The number of feeding shorebirds was scored every 15 min during low water. Based on literature (Goss-Custard et al., 1977; Zwarts et al., 1996; Kubetzki and Garthe, 2003; Folmer et al., 2010; Duijns et al., 2013) and personal observations (E. M. van der Zee), shorebirds species with cockles in their diet were divided in groups that prefer either adult cockles (> 12 mm; oystercatchers, herring gulls (*Larus argentatus*), common gull (*Larus canus*) and black headed gulls (*Larus ridibundus*)) or cockle recruits (< 12 mm; red knots, dunlins (*Calidris alpina*), bar-tailed godwits (*Limosa lapponica*) and curlews (*Numenius arquata*)). Birds were counted during 8 tidal cycles between June 2010 and May 2011 when bird densities in de Wadden Sea where highest.

2.3. Statistical analysis

For statistical comparisons, changes in adult cockles numbers were expressed as proportions relative to the initial numbers at the start of the experiment. To compare growth rate of cockles, we used the Bertalanffy's growth function (Von Bertalanffy, 1938). In this function, growth rate dH_t/dt declines with an increase in size H_t (the shell height in 2010) in the following way:

$$dH_t/dt = k (H_\infty - H_t) \quad (1)$$

where H_{∞} is the mean maximum size and k is the growth constant. For each individual cockle we estimated k by taking dH_t/dt as the difference in shell length between May 2011 and May 2010, H_t as shell height in May 2010 and H_{∞} as 45 mm (Cardoso et al., 2006). To deal with pseudoreplication (for having multiple cockles per enclosure) we averaged the growth constant k of cockles per plot.

To test for the general effects and their interaction of predation, density and site, we used general and generalized linear models. Prior to model fitting, all data were checked for normality and homogeneity of variance using Shapiro-Wilk tests ($p = .05$) and Bartlett's tests ($p = .05$) respectively. Therefore, we applied models with a Gaussian residual error distribution to changes in adult density, growth rate and plaster loss. Changes in adult cockle density were logit-transformed to obtain normality. Cockle recruitment could not be fitted to a Gaussian model. These data were therefore fitted to a Poisson regression model and a negative binomial model after which we selected the first model based on AIC comparisons. Models of which AIC differed > 2 from the parsimonious model were considered no substantial empirical support (Burnham and Anderson, 2002). Furthermore, to test for significance of the random effect the enclosure-control pairs, we first ran all above analyses with linear mixed-effects models (GLMM's) and repeated these procedures with linear models (GLM's) without the random effect pair. We selected models without random effects for all response variables based on AIC comparisons. For adult density, growth rate and plaster loss, we then used ANOVA tests (χ^2 Likelihood Ratio test). When applicable, we applied Tukey's HSD for post-hoc comparisons. Finally, bird observation data were analyzed with Chi-square tests.

All statistical analyses were carried out in R (R Development Core Team, 2014). GLMMs were constructed with the *glmmadmb* function in *glmmADMB* package. GLMs with negative binomial distributions were built with the *glm.nb* function from the *MASS* package. GLMs with Poisson error distributions, ANOVA models, post-hoc comparisons and Chi-squared test were constructed using the *glm*, *aov*, *TukeyHSD* and *chiq.test* functions from the *Stats* package (R Development Core Team, 2014).

3. Results

Adult cockle survival was significantly reduced by both high densities of cockles and predation by birds, the latter shown by the difference between controls and enclosures (Fig. 3A). However, cockle survival was overall lowered by 19% in the high density treatment compared to low density treatment at both sites (main effect of density: $F = 78.69$, $n = 24$, $p < .001$; $\bar{X}_{1000} \pm SE = 25.9 \pm 5.3\%$ vs. $\bar{X}_{100} \pm SE = 44.6 \pm 9.1\%$). Predation only negatively affected survival at the sandy site (interaction effect of site \times enclosure: $F = 5.19$, $n = 12$, $p = .03$; Tukey's HSD post-hoc test: site Sand, $p < .001$; site Mussel, $p = .11$) (Fig. 3A).

Growth rate of the tagged cockles was affected by site, density and predation (Fig. 3B). Cockle growth was 9% higher at the sandy site compared to the mussel wake site (main effect of site: $F = 19.99$, $n = 24$, $p < .001$; $\bar{X}_S \pm SE = 0.56 \pm 0.01 k$ vs. $\bar{X}_M \pm SE = 0.51 \pm 0.01 k$). Growth rates were significantly lower in the 1000 cockle m^{-2} than in the 100 cockle m^{-2} plots, but only when density was lowered by predation in the controls (interaction effect of density \times enclosure: $F = 10.17$, $n = 12$, $p = .003$; Tukey's HSD post-hoc test: predation in control plots, $p = .014$; predation in enclosure plots, $p = .55$).

Cockle recruitment was significantly correlated with predation and site, but not with density (Fig. 3C). Cockle recruit densities were 69% lower in the control than in the enclosure plots (main effect of enclosure: $\chi^2 = 33.2$, $df = 1$, $p < .001$; $\bar{X}_c \pm SE = 1.1 \pm 0.2 n m^{-2}$ vs. $\bar{X}_{ex} \pm SE = 3.6 \pm 0.7 n m^{-2}$) and 63% lower at site sand compared to the mussel site (main effect of site: $\chi^2 = 26.6$, $df = 1$, $p < .001$; $\bar{X}_S \pm SE = 1.3 \pm 0.3 n m^{-2}$ vs. $\bar{X}_M \pm SE = 3.5 \pm 0.7 n m^{-2}$).

Furthermore, there was a significant difference in hydrodynamics

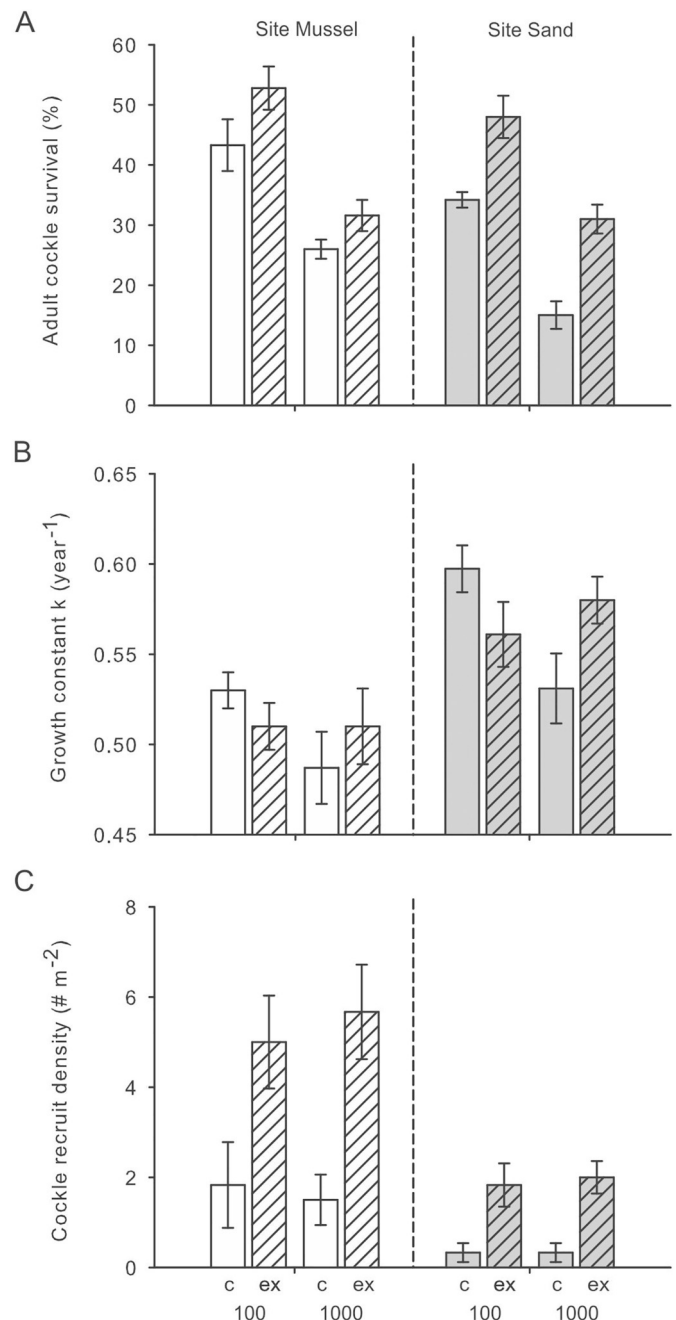


Fig. 3. Interaction plots showing (A) adult cockle survival after one year, (B) cockle growth after 1 year and (C) yearly cockle recruit density for the treatments: site, density and predation ($n = 6$ for each group). White bars represent the site in the vicinity of a mussel reef (site Mussel) and gray bars represent the site at a sandy intertidal flat (site Sand). Blank bars represent the control treatment (c) and striped bars represent the enclosure treatment (ex). Means ± 1 S.E.

between sites, with a higher relative weight loss of the plaster cylinders at the sand site compared to mussel site (main effect of site: $F = 28.73$, $n = 8$, $p < .001$; $\bar{X}_S \pm SE = 44.6 \pm 0.4\%$ vs. $\bar{X}_M \pm SE = 36.1 \pm 0.8\%$). We found no significant effects on plaster loss of enclosures (main effect of enclosure: $F = 0.02$, $n = 8$, $p = .89$; $\bar{X}_c \pm SE = 40.2 \pm 1.8\%$ vs. $\bar{X}_{ex} \pm SE = 40.4 \pm 1.9\%$) and cockle density (main effect of density: $F = 0.004$, $n = 8$, $p = .954$; $\bar{X}_{100} \pm SE = 40.3 \pm 1.7\%$ vs. $\bar{X}_{1000} \pm SE = 40.4 \pm 1.9\%$).

Observations of shorebirds foraging on adult-sized cockles resulted in a cumulative total density of 424 birds ha^{-1} over 8 tides, with a

density of 304 birds ha⁻¹ (63% oystercatchers, 32% herring gulls, 1% common gulls and 4% black headed gulls) at the mussel site and a density of 120 birds ha⁻¹ (20% oystercatchers, 7% herring gulls, 10% common gulls and 63% black headed gulls) at the sandy site ($\chi^2 = 40.99$, df = 1, $p < .001$). The density of shorebirds foraging on recruit-sized cockles was 504 birds ha⁻¹, with a density of 244 birds ha⁻¹ (16% red knots, 58% dunlins, 13% curlews and 13% bar-tailed godwits) at the mussel site and 260 birds ha⁻¹ (23% red knots, 6% dunlins, 2% curlews and 69% bar-tailed godwits) at the sandy site ($\chi^2 = 0.19$, df = 1, $p = .66$).

4. Discussion

Although predation, competition, habitat characteristics and their combined effects have been recognized as important structuring mechanisms in ecosystems, the interplay between the three types of interaction on population dynamics have hardly been investigated to our knowledge. In this study, we demonstrate that cockles, one of the most common and important prey species in the Wadden Sea (e.g. Verwey, 1981; van Gils et al., 2006; Compton et al., 2013), are influenced by habitat characteristics that affect survival, growth and predation risk across different life stages. Similar in how other foundation species, like seagrasses, for example, mitigate predation (i.e. Reise, 1985). Our experimental results show that cockles have higher recruit and adult survival in the wake of a 1-ha mussel bed, due to reduced hydrodynamics, as hydrodynamic stress can have positive effect on recruitment and persistence over a large spatial scale (see for extensive discussion for this site in: Donadi et al., 2013a). Moreover, despite the generally higher abundance of shorebirds foraging on adult cockles at the mussel site, our results show a lower predation pressure on adult cockles at this site. This might be caused by the high adult cockle densities (i.e., caused by the enhanced recruitment and adult survival) in combination with high densities of other potential prey (i.e., mussels), which seems to mitigate potential predation effects of this increased shorebird abundance as there is overall more prey to feed on. Apart from these positive effects of the habitat conditions created by mussels, it negatively affected relative growth rates of cockles, an effect that is most likely caused by reduced water flow (and hence lower food availability) (Frechette et al., 1989) and by indirectly affecting interspecific competition for food (Donadi et al., 2013a) through the facilitation of cockles.

The low impact of predation on adult cockles at the mussel site compared to the control site can be explained as earlier studies suggested (Charnov, 1976; Olsson and Molokwu, 2007) and demonstrated (Brown, 1988) that predators have higher giving-up-densities (GUD) in higher quality foraging environments. At the mussel site, with high cockle densities and mussels nearby as an alternative prey for molluscivore shorebird that forage on adult-sized cockles, higher intake rates may induce higher GUDs and hence a reduced predation effect compared to the sandy site where bivalve prey was much less abundant. Our results correspond to this explanation by showing that numbers of remaining cockles in the control plots at the mussel site were higher for both manipulated densities compared to numbers of remaining cockles in the control plots at the sandy site (Fig. 3A).

In contrast to predation on adult cockles, we found no significant site effect of predation on recruits (i.e. no interaction between site and enclosure on recruit densities). As the number of cockle recruits were relatively low at both sites, it seems likely that a lack of alternative prey for birds specifically feeding on this size class, results in lower GUDs at both sites (lower recruit densities), causing the observed differential result on predation between recruits and adult cockles. Another explanation for this result might be that red knots, which are important avian predators of small cockles, have much larger home ranges (van Gils and Piersma, 1999), than oystercatchers (Schwemmer and Garthe, 2011) and that predation was much lower on small cockles. This suggests that the notion that environments differ between both sites may

only hold for oystercatchers and not for red knots. For this reason, one would only expect a differential predation effect between sites for adult cockles, but not for recruits. The overall low densities of cockle recruits further indicates low survival during the first months after settlement, most likely due to predation by crabs and shrimps that were able to enter the enclosures and are known to strongly reduce cockle spat numbers (e.g. Strasser, 2002; van der Heide et al., 2014).

Apart from competition for food between mussels and cockles at the mussel site (Donadi et al., 2013a), we found a significant effect of cockle density on adult cockle survival and growth. The lower survival of adult cockles in the high density treatments is most likely caused by intraspecific competition for space as cockles need to be buried at the surface of the sediment to filter feed with their short siphons (see for example for an other bivalve species Peterson and Andre, 1980) and/or by density-dependent predation by crabs (Seitz et al., 2001). It is not caused by density-dependent predation by shorebirds because we did not detect a difference in density-dependent survival between the enclosure and control plots. Note that crabs can enter these enclosures and birds do not enter. The density-dependent effect on growth under normal conditions (i.e. including predation), however, cannot solely be explained by intraspecific competition for food. The lack of a density-effect in enclosures indicates that the 1-m² plots were probably too small to cause significant differences in food depletion between the high and low density treatment (Kamermans et al., 1992, but see for example Peterson, 1982) or that treatment densities were too low to see an effect of food depletion (Jensen, 1992, 1993). We therefore suggest that the density-dependent effect on growth in the presence of predators and the lack of this effect in the absence of predators is a behavioral mechanism in response to predators (Brown and Kotler, 2004 and references therein, Compton et al., 2016) rather than an effect of food depletion. Possibly, cockles in the enclosure plots bury less deeply, as there is no need to escape predation (but see Zwartz and Wanink, 1989; Griffiths and Richardson, 2006). A more shallow position would make it easier to filter-feed and by reducing burrowing activities, less encounters with conspecifics would occur, resulting in longer feeding times (Peterson and Andre, 1980). This effect can especially increase growth rate in the high densities plots with high encounter rates, thereby neutralizing the density-dependent effect of 1000 versus 100 cockles per m². Other behavioral responses of cockles to shorebird predation might be an extension of their valve closure time during low tide and/or the investment in thicker shelves (Irlandi and Peterson, 1991; Smith and Jennings, 2000). The absence of these responses when avian predators are excluded might neutralize the density-dependent effect on growth as well, but only if shorebird predation is density-dependent. For this hypothesis, however, we did not find evidence, since density-dependent survival did not differ between the enclosure and control plots (but see for example Goss-Custard, 1977). Overall, we demonstrate that predation increases the strength of intraspecific competition.

Recently, integration of multiple interaction types into so-called "interaction networks" has been gaining attention (Christianen et al., 2017; Borst et al., 2018), but the studies addressing this issue have mostly remained of a theoretical nature (e.g. Goudard and Loreau, 2008; Keffi et al., 2012). Our empirical results clearly show that predation, competition and habitat characteristics can interactively control population dynamics in a real ecosystem, which emphasizes the need to integrate multiple ecological interaction types into a single framework (Olff et al., 2009). Finally, our study shows that communities in intertidal soft-sediment ecosystem can be strongly structured by ecosystem engineers. We therefore argue that conservation and restoration of habitat-forming species like mussels, oysters and seagrasses is crucial for protecting the health and overall functioning of these ecosystems.

Declaration of Competing Interest

None.

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